

An exceptionally rich Soricidae (Mammalia) fauna from the upper Miocene localities of Polgárdi (Hungary)

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(with 8 figures, 11 tables and 2 plates)

Abstract

More than 7000 shrew specimens were found in the Upper Miocene localities of Polgárdi, Hungary. The well preserved bones and teeth were deposited mainly by pit-fall accumulations. *Crusafontina kormosi* (BACHMAYER & WILSON), *Amblycoptus oligodon* KORMOS, *Kordosia topali* (JÁNOSSY), *Blarinella dubia* (BACHMAYER & WILSON), *Asoriculus gibberodon* (PETÉNYI), *Zelceina soriculoides* (SULIMSKI) and *Paenelimnoecus repenningi* (BACHMAYER & WILSON) were identified from the samples. On the basis of these occurrences, all sites belong to the Late Turolian MN 13 Zone, but locality 4 is somewhat older, and locality 2 is earlier than locality 5. The soricids suggest that Polgárdi 2 and 4 were well watered, forested areas in semiarid climate, while Polgárdi 5 might have been an open environment in a karstic grassland area.

Introduction

The richness and the state of preservation of the Polgárdi fossil fauna is particular even on a world-scale. The Polgárdi limestone quarry, as a Neogene locality, was discovered by L. LÓCZY, the first report on the sites was given by KORMOS (1911). In 1926 he described a new shrew genus and species from Polgárdi, locality 2. KRETZOI (1942, 1952) mentioned many carnivore species from this "Hipparion-fauna". KORDOS (1985, 1987) and FREUDENTHAL & KORDOS (1989) described new rodent genera and species from different sites of Polgárdi. BOLKAY (1913), FEJÉRVÁRY (1917), FEJÉRVÁRY-LÁNGH (1923) and VENCEL (1994, 1997) wrote up the reptiles and the amphibians, JÁNOSSY (1991) treated the birds. Further contributions are by KORMOS (1913, 1914) and KRETZOI (1983). KORDOS (1991 a) summarized the history and the geological background of the localities. The present author in his systematic papers already mentioned two Anourosoricini shrews from Polgárdi 4 and 5 (MÉSZÁROS 1997, 1998 b), while the whole soricid fauna is presented here.

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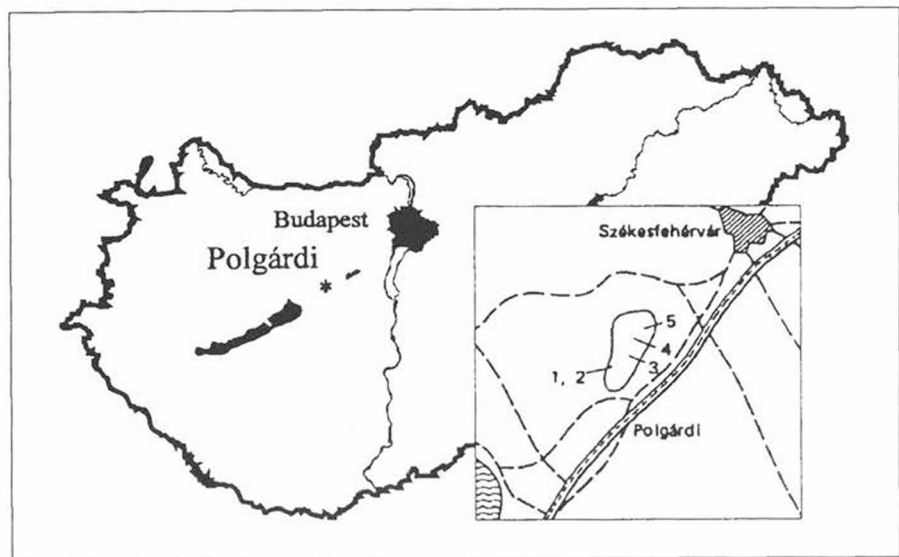


Fig. 1. Geographic situation of the Polgárdi fossil localities.

Localities

In the Devonian crystalline limestone of the Kőszár Hill, near Polgárdi (Fejér County), a great number of karstified fissures and caves were excavated by the large-scale exploitation of the rock. In the quarry, between 1909 and 1991, five localities (Fig. 1) were discovered with rich and excellently preserved fauna. The sorcid remains came from locality 2, 4 and 5.

Locality 2. In the relevant literature this site is, in general, referred to as locality Polgárdi. During the excavation performed by T. KORMOS in 1910, bone remains were collected from a surface hall of a large sinkhole cave. In the profile of the cave-deposit, containing rich hipparion fauna, five beds were distinguished. Unfortunately KORMOS did not separated the fossils from these different layers. As far as we can judge now, they all represent the same biostratigraphical level (FREUDENTHAL & KORDOS 1989).

Locality 4. An inverse Y-shaped karstic fissure was discovered by I. DUNKL and S. JÓZSA in 1984 in the eastern wall at the lower level of the operating limestone quarry. L. KORDOS, with the help of the discoverers, removed all the sediments in 1984-1985. During the collecting work, the so-called "lower" and "upper" localities were distinguished. According to FREUDENTHAL & KORDOS (1989) and KORDOS (1991a), these two sites belong to the same fissure system, and they appear to be of the same age.

Locality 5. In 1985 a great number of vertebrate remains were found in the fill of a large fossil cave, at a level 15 m higher than locality 4, and about 250 m north-east of the previous site. The material was collected by L. KORDOS. This was the richest finding among the Polgárdi fossils.

KORMOS (1911 and 1926) reported three Soricidae from Polgárdi 2 site:

Sorex sp.

Crocidura sp.

Amblyoptus oligodon n. g. et n. sp.

The present study has resulted in the following list of identified species from the discussed sites:

Polgárdi 2

Amblyoptus oligodon KORMOS, 1926

Blarinella dubia (BACHMAYER & WILSON, 1970)

Paenelinnoecus repenningi (BACHMAYER & WILSON, 1970)

Polgárdi 4

Crusafontina kormosi (BACHMAYER & WILSON, 1970)

Amblyoptus oligodon KORMOS, 1926

Blarinella dubia (BACHMAYER & WILSON, 1970)

Zelceina soriculoides (SULIMSKI, 1959)

Asoriculus gibberodon (PETÉNYI, 1864)

Paenelinnoecus repenningi (BACHMAYER & WILSON, 1970)

Polgárdi 5

Blarinella dubia (BACHMAYER & WILSON, 1970)

Kordosia topali (JANOSSY, 1972)

Species	Polgárdi 2		Polgárdi 4		Polgárdi 5	
	A	B	A	B	A	B
<i>C. kormosi</i>	-	-	149	56	-	-
<i>A. oligodon</i>	9	2	156	61	-	-
<i>K. topali</i>	-	-	-	-	608	156
<i>B. dubia</i>	15	7	237	102	5683	2452
<i>A. gibberodon</i>	-	-	87	41	-	-
<i>Z. soriculoides</i>	-	-	7	4	-	-
<i>P. repenningi</i>	1	1	22	15	-	-
unidentifiable 1*	-	-	30	-	-	-
unidentifiable 2**	-	-	68	-	-	-
Isolated teeth (%)	24.00	-	8.57	-	1.84	-

Table 1. Catalogue of the Polgárdi Soricidae remains. A = number of specimens, B = minimum number of individuals, unidentifiable shrews, without the main differential characters: * = in the size of *Paenelinnoecus repenningi*, ** = in the size of *Blarinella dubia*, *Asoriculus gibberodon* and *Zelceina soriculoides*.

Material and methods

All studied specimens are stored in the collection of the Geological Museum of Hungary (GMH, in the Hungarian Geological Institute). The catalogue of the whole

soricid material includes 7072 specimens (Tab. 1). The author selected the shrew remains from the Polgárdi 4 and 5 samples, washed by a team of the Hungarian Geological Institute. The Polgárdi 2 soricids were catalogued in the collection as KORMOS determined them.

The SEM photos were made in the Microsonda Laboratory of the Geological Institute, Eötvös Loránd University.

The morphological terms and the measurements (in mm) are used after REUMER (1984) and MÉSZÁROS (1996).

Systematic palaeontology

Class Mammalia LINNAEUS, 1735

Order Insectivora BOWDICH, 1821

Family Soricidae GRAY, 1821

Subfamily Soricinae FISCHER VON WALDHEIM, 1817

Tribe Anourosoricini ANDERSON, 1879

Genus *Crusafontina* GIBERT, 1974

Type species. *Crusafontina endemica* GIBERT, 1974

Crusafontina kormosi (BACHMAYER & WILSON, 1970)

Text-Fig. 2, Pl. 2, Fig. 10

1954 - *Amblycoptus vicinus* n. sp. - KRETZOI, p. 49 (Csákvár)

1970 - *Anourosorex kormosi* nov. spec. - BACHMAYER & WILSON, p. 551, figs 3-4a, 20-20a, 21-25 (Kohfidisch)

1978 - *Anourosorex kormosi* BACHMAYER & WILSON, 1970 - BACHMAYER & WILSON, p. 141 pl. 2, figs. 5-5a (Kohfidisch)

1978 - "*Anourosorex*" *kormosi* BACHMAYER & WILSON, 1970 - STORCH, p. 424, pl. 4, figs 29-39 (Dorn-Dürkheim)

1980 - *Anourosorex kormosi* BACHMAYER & WILSON, 1970 - BACHMAYER & WILSON, p. 361 (Kohfidisch)

1996 - *Crusafontina vicina* (KRETZOI, 1954) - MÉSZÁROS, p. 9, pl. 12, figs 5 a-b (Csákvár)

1998 a - *Crusafontina kormosi* (BACHMAYER & WILSON, 1970) - MÉSZÁROS, p. 106, pl. 1, figs 5-11 (Tardosbánya)

Holotype. Right lower jaw with the complete dentition, BACHMAYER & WILSON (1970), p. 551, Pl. 1, fig 3, Natural History Museum, Vienna (NHMV), Div. Geol. Paleont. 1970/1389. Type locality: Kohfidisch (Austria, Late Vallesian, MN 10).

Stratigraphical range. Late Miocene (Late Vallesian, MN 10 - Late Turolian, MN 13), Europe.

Studied material. Polgárdi 4: 11 fragmentary skulls, 12 left and 9 right maxillary fragments, 56 left and 39 right mandibles, 2 left and 11 right I¹, 1 left P⁴, 3 left and 4 right I₁. Figured specimens: GMH, V. 20717. and V. 20718.

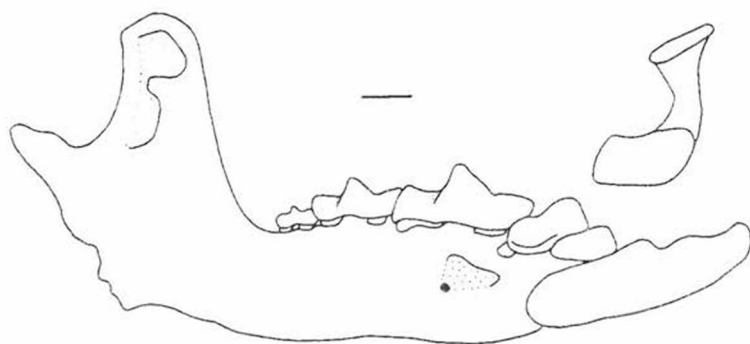


Fig. 2. *Crusafontina kormosi* (BACHMAYER & WILSON, 1970). GMH V. 20717., loc. Polgárdi 4 "upper", right mandible, lateral view and the condyle, posterior view, scale bar = 1 mm.

		min.	mean	max.	spec. nr.	standard error	standard deviation
I ¹	L	2.20	2.45	2.76	12	0.1267	0.1533
	H	1.66	1.84	2.00	12	0.0653	0.0826
A ¹	L	1.50	1.78	2.12	21	0.1525	0.1740
	W	1.10	1.27	1.70	21	0.0906	0.1305
A ²	L	0.95	1.05	1.20	22	0.0529	0.0673
	W	0.90	1.03	1.12	22	0.0596	0.0675
P ⁴	LL	1.45	1.73	1.96	44	0.0773	0.1029
	BL	2.35	2.56	2.80	44	0.0821	0.1002
	W	2.00	2.33	2.90	44	0.1773	0.2167
M ¹	LL	1.45	1.82	2.28	41	0.0839	0.1258
	BL	1.90	2.15	2.56	41	0.0977	0.1239
	AW	1.90	2.22	2.58	41	0.1205	0.1478
	PW	1.70	2.01	2.36	41	0.1154	0.1462
M ²	LL	1.08	1.17	1.38	9	0.0667	0.0879
	BL	1.20	1.29	1.39	9	0.0556	0.0622
	AW	1.82	2.01	2.18	9	0.0815	0.1007
	PW	1.12	1.20	1.32	9	0.0444	0.0573
I ₁	L	4.81	5.14	5.56	6	0.2356	0.2736
	H	1.10	1.28	1.52	6	0.1067	0.1332
M ₁	L	2.50	2.72	3.20	87	0.0924	0.1222
	W	1.16	1.37	4.64	87	0.0567	0.0772
M ₂	L	1.20	1.88	2.28	65	0.1228	0.1771
	W	0.88	1.12	1.36	65	0.0511	0.0751
M ₃	L	0.90	1.04	1.34	33	0.0683	0.0932
	W	0.46	0.63	0.84	33	0.0610	0.0848

Table 2. Measurements of *Crusafontina kormosi* (BACHMAYER & WILSON, 1970) from Polgárdi 4, after MÉSZÁROS 1998 b.

Measurements. See Tab. 2.

Remarks. The detailed description of *C. kormosi* from Polgárdi is given in the special publication of the author (MÉSZÁROS, 1998 b), in which he elaborates the *Crusafontina* remains of five Hungarian Late Miocene localities. In this work all described *Crusafontina* forms are ranged into *C. endemica* GIBERT, 1974 or *C. kormosi* (BACHMAYER & WILSON, 1970), and the differential characters between the two species are given. Mainly on the basis of the M_3 morphology, the M_2/M_3 length ratio, the I^1 measurements, the Polgárdi *Crusafontina* is referred to the latter one.

Genus *Amblyoptus* KORMOS, 1926

Type species. *Amblyoptus oligodon* KORMOS, 1926.

Amblyoptus oligodon KORMOS, 1926

Text-Fig. 3, Pl. 2, Figs 4-7

- 1926 - *Amblyoptus oligodon* n. g. et n. sp. - KORMOS, p. 543, pl. 3, figs 1-5 (Polgárdi 2)
 1980 - *Amblyoptus* cf. *oligodon* KORMOS, 1926 - KRETZOI, p. 312 (Széchenyi Hill)
 1995 - *Amblyoptus* cf. *oligodon* KORMOS, 1926 - HIR & MÉSZÁROS, p. 171, figs 4 a-l (Egyházasdengeleg)
 1996 - *Amblyoptus oligodon* KORMOS, 1926 - MÉSZÁROS, p. 9, pl. 1, figs 2 a-b (Széchenyi Hill)
 1998 - *Amblyoptus oligodon* KORMOS, 1926 - MÉSZÁROS, p. 104, pl. 1, figs 1-4 (Tardosbánya)

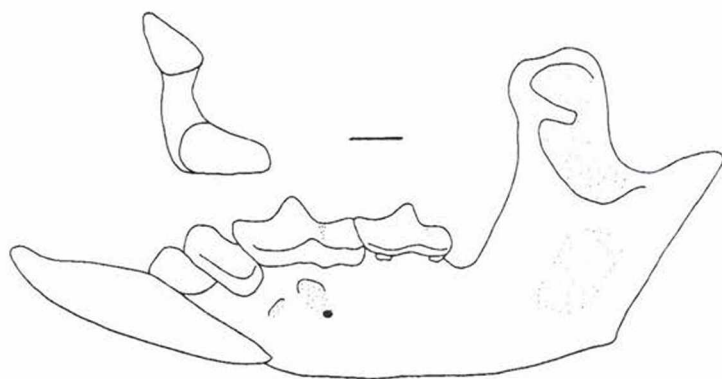


Fig. 3. *Amblyoptus oligodon* KORMOS 1926. GMH V. 20720., loc. Polgárdi 4 "upper", left mandible, lateral view and the condyle, posterior view; scale bar = 1 mm.

Holotype. Left maxilla with five teeth, Geological Museum of Hungary, OB. 5071., KORMOS (1926), p. 352, pl. 3, figs 1-5., Type locality: Polgárdi 2. (Hungary, Late Turolian, MN 13).

Stratigraphical range. Late Miocene (Turolian, MN 12-13), Europe.

Studied material. Polgárdi 4: 8 fragmentary skulls, 4 left and 3 right maxillary fragments, 53 left and 52 right mandibles, 6 left and 6 right I^1 , 1 left A^1 , 8 left and 13 right I_1 , 1 right M_1 , 1 left M_2 . Figured specimens: GMH, V. 20719. and V. 20720. Polgárdi 2: 1 left maxilla (the holotype), OB. 5071., 2 mandibles, 2 M_1 , 4 I_1 .

Measurements. See Tabs 3-4.

Description. The sagittal crest of the skull terminates between the little frontal foramina. The infraorbital fossa is very deep. The palatine foramina are situated at the middle of A^1 . The palatine fossa is short and broad. The top of the coronoid process is widened in most mandibles. The upper part of the external temporal fossa is deep, the lower one is shallower, the coronoid spicule is long and high. The ascending and horizontal rami form a slightly obtuse angle, the lower margin of the horizontal one is convex. The mental foramen is placed under the re-entrant valley of M_1 . A subdivided muscular depression is situated under and before the foramen. The upper articular facet of the condyle is triangular, the lower one is mesially oblong, the interarticular area is extremely narrow. The external pterygoid fossa is deep and broad. The internal temporal fossa is oval, tight and deep, the mandibular foramen is placed under the middle or the posterior part of its lower margin. Dental formula is 142/122, the third molars are always missing. There is a buccal cingulum and conule in the basal margin of the upper incisor. A^1 is a long-crowned, big tooth with posteriorly widened cingula in both sides. There is no parastyle before the large paracone. We can see a tiny hypocone in the postero-lingual corner, and a somewhat bigger protocone before it. The second upper antemolar is triangular and far smaller than the first one. The big paracone is in central position, cingula are well-developed in the lingual and the buccal side. A^3 is tiny and unicuspid. The P^4 parastyle is protruding, it is contacted with the paracone by a weak parastylar crest. The paracone and the well-developed hypocone are separated by a deep valley. The hypoconal flange is long, a minute cuspule is risen in the lingual ridge. The posterior margin is deeply notched. The buccal edge is long and sharp. The PW of M^1 is somewhat less than AW, the parastyle is strong, the metastyle is much weaker, the mesostyle is hardly-developed. The trigone is posteriorly closed by a wide metaloph. The hypocone is well-developed, the hypoconal flange is shorter than in P^4 , the posterior emargination is deeply notched. M^2 is reduced, triangular. The trigone is basined, the parastyle is long. The hypocone, the protocone and the metacone are well-identifiable. The mandibular incisor is strong and acuspulate, its apex is not up-curved. The cingulum may be present or missing in the lower antemolars and molars. The antemolars are unicuspid, A_1 is far smaller than A_2 . The entoconid and the entostylid are separated by a tight valley in the mandibular molars. The entoconid crest is present in both teeth. The M_2 talonid is basined, the hypoconid and the entoconid are well-developed.

Remarks. After that MÉSZÁROS (1997) distinguished *Kordosia* from this genus, it contains only one species. All hitherto known, well documented occurrences of this form are from the Carpathian Basin, thus *Amblycoptus* seems to be an endemic and monospecific group.

		min.	mean	max.	spec. nr.
A ¹	L	1.93	1.75	2.10	2
	H	1.35	1.53	1.70	2
A ²	L	0.90	0.95	1.00	2
	W	1.30	1.30	1.30	2
P ⁴	LL	1.85	1.90	1.95	2
	BL	2.50	2.65	2.80	2
	W	2.60	2.75	2.90	2
M ¹	LL	2.25	2.25	2.25	2
	BL	2.30	2.33	2.35	2
	AW	2.65	2.68	2.70	2
	PW	2.15	2.20	2.25	2
M ₁	L	1.87	2.75	2.85	2
	W	1.00	1.35	1.70	2

Table 3. Measurements of *Amblycoptus oligodon* KORMOS 1926 from Polgárdi 2.

		min.	mean	max.	spec. nr.	standard error	standard deviation
A ¹	L	1.70	1.82	2.00	9	0.0889	0.1054
	H	1.25	1.31	1.35	9	0.0346	0.0393
A ²	L	0.80	0.93	1.05	11	0.0835	0.0911
	W	0.95	1.02	1.15	11	0.0471	0.0579
P ⁴	LL	1.50	1.64	1.85	18	0.0852	0.0990
	BL	2.30	2.46	2.60	18	0.0722	0.0891
	W	2.25	2.38	2.55	18	0.0722	0.0870
M ¹	LL	1.80	2.07	2.45	17	0.0834	0.1152
	BL	2.16	2.37	2.51	17	0.1179	0.1288
	AW	2.00	2.34	2.65	17	0.1219	0.1382
	PW	1.98	2.08	2.00	17	0.0580	0.0705
M ₁	L	2.50	2.77	3.00	65	0.1174	0.1438
	W	1.28	1.45	1.65	65	0.0976	0.1137

Table 4. Measurements of *Amblycoptus oligodon* KORMOS 1926 from Polgárdi 4.

Genus *Kordosia* MÉSZÁROS, 1997

Type species. *Amblyoptus topali* JÁNOSSY, 1972.

Kordosia topali (JÁNOSSY, 1972)

Text-Fig 4, Pl. 2, Figs 1-3

1972 - *Amblyoptus topali* sp. n. - JÁNOSSY, p. 38, pl. 3, figs 7-10 (Osztramos 1)

1975 - *Amblyoptus* cf. *topali* JÁNOSSY, 1972 - RZEBIK-KOWALSKA, p. 178, fig. 4 (Zamkova Dolna)

1979 - *Amblyoptus topali* JÁNOSSY, 1972 - SULIMSKI et al., p. 387 (Mala Cave)

1984 - *Amblyoptus topali* JÁNOSSY, 1972 - REUMER, p. 110 pl. 35, figs 7-9, plate 36, figs 1-3 (Osztramos 1)

1984 - *Amblyoptus* sp. - REUMER, p. 113, plate 35, fig 10 (Osztramos 7)

1997 - *Kordosia topali* JÁNOSSY, 1972 - MÉSZÁROS, p. 72, figs 5-7 (Polgárdi 5)

Holotype. Right mandible with the incisor, the two antemolars, the first molar and the alveoli of the second one. Hungarian Natural History Museum, V. 71. 49., JÁNOSSY, 1972, p. 38, pl. 3, figs 6-10. Type locality: Osztramos 1 (Hungary, Early Ruscinian, MN 14).

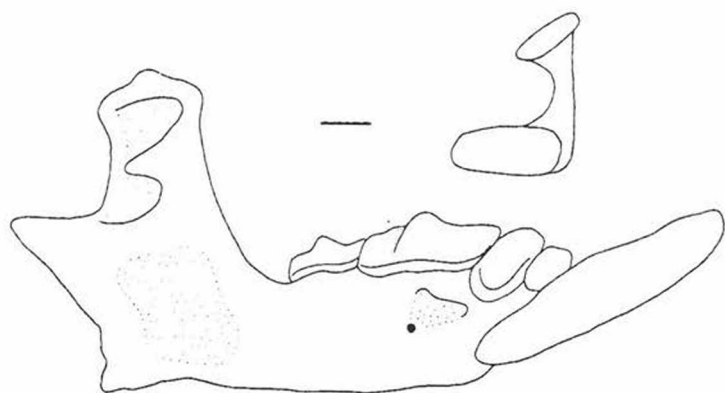


Fig. 4. *Kordosia topali* (JÁNOSSY, 1972). GMH V. 20721., loc. Polgárdi 5, right mandible, lateral view and the condyle, posterior view, scale bar = 1 mm.

Stratigraphical range. Late Miocene (Turolian, MN 13) - Late Pliocene (Villányian, MN 16), Europe.

Studied material. Polgárdi 5: 49 complete or fragmentary skulls, 39 left and 49 right maxillae or maxillary fragments, 174 left and 181 right mandibles or mandible fragments, 29 left and 40 right I^1 , 4 right A^1 , 2 left and 2 right P^4 , 4 left and 2 right M^1 , 2 left and 3 right M_1 , 1 left M_2 , 11 left and 16 right I_1 . Figured specimens: GMH, V. 20721.

Measurements. See Tab. 5.

		min.	mean	max.	spec. nr.	standard error	standard deviation
A ¹	L	1.80	2.16	2.50	87	0.1237	0.1576
	W	1.10	1.50	1.80	87	0.0986	0.1431
A ²	L	0.80	1.13	1.70	106	0.0968	0.1312
	W	0.85	1.17	1.40	106	0.0891	0.1098
P ⁴	BL	2.00	2.23	2.95	141	0.1464	0.2156
	LL	2.10	2.68	3.10	141	0.1424	0.1963
	W	2.10	2.51	2.90	141	0.1111	0.1479
M ¹	BL	1.90	2.15	2.50	117	0.1071	0.1311
	LL	2.05	2.44	2.70	117	0.0984	0.1277
	AW	2.10	2.70	3.05	117	0.1094	0.1524
	PW	1.90	2.25	2.60	117	0.1280	0.1548
M ₁	L	2.60	3.03	3.50	225	0.1064	0.1368
	W	1.05	1.54	1.80	225	0.0656	0.0870

Table 5. Measurements of *Kordosia topali* (JÁNOSSY, 1972) from Polgárdi 5, after MÉSZÁROS 1997.

Remarks. JÁNOSSY (1972) described the new Anourosoricini shrew species, what has been found in Osztramos 1, Hungary, as *Amblyoptus topali*. MÉSZÁROS (1997) studied a larger *topali* material from Polgárdi 5. According to the detailed morphological researches, in many characters the species seemed different from the European *Amblyoptus*, while similar to the Asian *Anourosorex*. MÉSZÁROS (1997) established a new genus, *Kordosia* for this specially adapted soricid. According to his differential diagnosis for *Kordosia*, this genus differs from *Amblyoptus* in missing of A³, its larger size, the tighter internal temporal fossa, the present parastyle of A¹, the more anteriorly situated hypocone of A², the oblong shaped P⁴, and the less PW of M¹. It is distinguished from *Anourosorex* mainly in the lack of the little M³ and M₃ and acusculate structure of I₁, from *Paranourosorex* in lacking of A³, M³ and M₃ and acusculate structure of I₁. *Kordosia* has the most reduced dental formula in the tribe Anourosoricini: 132/122. A³, M³ and M₃ is always missing. The genus contains also *K. jessiae* described from Maramena (Greece) by DOUKAS (DOUKAS *et al.* 1995). *K. topali* differs from *K. jessiae* in the larger size, the L/W ratio of M₁ and the different morphology of I¹.

Tribe Soricini FISCHER VON WALDHEIM, 1817
Genus *Blarinella* THOMAS, 1911

Type species. *Blarinella quadratauda* MILNE-EDWARDS, 1872

Blarinella dubia (BACHMAYER & WILSON, 1970)

Pl. 1, Figs 1-3, Pl. 2, Figs 11-12

- 1911 - *Crociodura* sp. - KORMOS, p. 57 (Polgárdi 2)
 partim 1954 - *Soricidarum* g. et sp. indet. II. - KRETZOI, p. 49. (Csákvár)
 1970 - *Petenya dubia* n. spec. - BACHMAYER & WILSON, p. 546. figs 6, 26, 27, 30, 31a (Kohfidisch)
 1976 - *Petenya dubia* BACHMAYER & WILSON, 1970 - KRETZOI et al., p. 375 (Rudabánya)
 1978 - *Petenya dubia* BACHMAYER & WILSON, 1970 - BACHMAYER & WILSON, p. 138, fig. 18 (Kohfidisch)
 1984 - *Petenya dubia* BACHMAYER & WILSON, 1970 - KRETZOI, p. 216 (Sümeg)
 1984 - *Blarinella dubia* (BACHMAYER & WILSON, 1970) - REUMER, p. 66 pl. 20 figs 5-8 (Osztramos 9)
 1985 - *Blarinella dubia* (BACHMAYER & WILSON, 1970) - RABEDER, p. 447 (Rudabánya)
 1989 - *Blarinella dubia* (BACHMAYER & WILSON, 1970) - RZEBIK-KOWALSKA, p. 533 fig. 3 (Podlesice, Zalesiaki 1B)
 1991 b - *Blarinella dubia* (BACHMAYER & WILSON, 1970) - KORDOS, p. 348 (Rudabánya)
 1995 - *Blarinella* cf. *dubia* (BACHMAYER & WILSON, 1970) - Hír & MÉSZÁROS, p. 171, figs. 3 c-d (Egyházasdengeleg)
 1996 - *Blarinella dubia* (BACHMAYER & WILSON, 1970) - MÉSZÁROS, p. 13, pl. 3, figs 6 a-g (Sümeg, Csákvár)
 1998 - *Blarinella dubia* (BACHMAYER & WILSON, 1970) - MÉSZÁROS, p. 107, pl. 2, figs 1-10 (Tardosbánya)

		min.	mean	max.	spec. nr.	standard error	standard deviation
P ⁴	LL	-	1.26	-	1	-	-
	BL	-	1.03	-	1	-	-
	W	-	1.45	-	1	-	-
M ¹	LL	-	1.48	-	1	-	-
	BL	-	1.43	-	1	-	-
	AW	-	1.30	-	1	-	-
	PW	-	1.40	-	1	-	-
I ₁	L	-	4.14	-	1	-	-
	H	-	0.88	-	1	-	-
M ₁	L	1.50	1.56	1.63	8	0.0463	0.0492
	W	0.87	0.92	1.00	8	0.0349	0.0402
M ₂	L	1.35	1.40	1.45	8	0.0325	0.0367
	W	0.79	0.87	0.94	8	0.0369	0.0465
M ₃	L	1.05	1.09	1.15	4	0.0350	0.0394
	W	0.63	0.64	0.65	4	0.0050	0.0071

Table 6. Measurements of *Blarinella dubia* (BACHMAYER & WILSON, 1970) from Polgárdi 2.

Holotype. Left mandible fragment with the three molars, NHMV, Div. Geol. Paleont., 1970/1387. (BACHMAYER & WILSON 1970, p. 546, fig. 6.) Type locality: Kohfidisch (Austria, Late Vallesian, MN 10).

Stratigraphical range. Late Miocene (Early Vallesian, MN 9) - Early Pliocene (Early Ruscinian, MN 14), Europe.

Studied material. Polgárdi 2: 1 right maxilla fragment, 8 left and 6 right mandible fragments. Polgárdi 4: 12 skull fragments, 13 left and 14 right maxillary fragments, 102 left and 83 right maxillae, 3 right and 2 left I^1 , 1 left P^4 , 1 right P^4 , 1 right I_1 , 1 right A_2 , 1 left and 3 right M_1 . Polgárdi 5: 139 skulls, 304 left and 316 right maxillae, 2420 left and 2504 right mandibles. Figured specimens: GMH, V. 20723.

Measurements: See Tabs 6-8.

		min.	mean	max.	spec. nr.	standard error	standard deviation
I^1	L	2.00	2.23	2.52	4	0.2200	0.2256
	H	1.28	1.29	1.32	4	0.0138	0.0164
P^4	LL	0.98	1.06	1.08	4	0.0375	0.0433
	BL	1.43	1.55	1.66	4	0.0750	0.0850
	W	1.35	1.53	1.66	4	0.1150	0.1143
M^1	LL	1.35	1.45	1.53	5	0.0424	0.0588
	BL	1.40	1.52	1.63	5	0.0624	0.0763
	AW	1.39	1.50	1.55	5	0.0424	0.0557
	PW	1.45	1.56	1.66	5	0.0496	0.0673
M^2	LL	1.23	1.32	1.55	5	0.0928	0.1189
	BL	1.15	1.32	1.48	5	0.0776	0.1057
	AW	1.23	1.51	1.63	5	0.1224	0.1484
	PW	4.35	1.46	1.50	5	0.0440	0.0555
M^3	L	0.55	0.59	0.63	4	0.0400	0.0400
	W	1.28	1.34	1.39	4	0.0475	0.0482
I_1	L	3.44	3.66	3.88	4	0.1600	0.0709
	W	0.55	0.84	0.96	4	0.0438	0.1692
M_1	L	1.45	1.58	1.69	8	0.0497	0.0663
	W	0.85	1.91	0.94	8	0.0291	0.0314
M_2	L	1.35	1.42	1.53	8	0.0491	0.0586
	W	0.84	0.85	0.89	8	0.0325	0.0354
M_3	L	1.05	1.13	1.18	8	0.0312	0.0396
	W	0.60	0.67	0.98	8	0.0800	0.1196

Table 7. Measurements of *Blarinella dubia* (BACHMAYER & WILSON, 1970) from Polgárdi 4.

Description. The skull is elongated, without sagittal crest. The fossa infraorbitale is extremely deep. The external temporal fossa on the mandible usually extends ventrally to the level of the centre, but sometimes only to the top of the condyle. The spiculum coronoideum is slightly-developed. The upper articular facet of the condyle is cylinder-shaped and makes an angle of about 45° with the lower facet. The interarticular area is broad. The internal temporal fossa is triangular, high, and usually subdivided by a horizontal bar. The mandibular foramen is situated at the middle of the fossa. The mental foramen is placed under the re-entrant valley of M_1 . Dental formula is

163/123. The upper incisor is not fissident. Its superior and posterior margins form a right angle. There is a broad buccal cingulum along the convex basal margin. The top of the apex and the talone are sharp and whitely coloured, the apex is long and down-curved. There are five antemolars present, decreasing in size from the first to the last, in the maxilla. All of them have a little second cusp beside the main cone, on the lingual cingulum. In P^4 the lingually placed parastyle is contacted with the paracone by a parastylar crest. The protocone forms an antero-lingual corner. The hypocone is only slightly raised from the ridge of the extended hypoconal flange. The posterior emargination is hardly notched. The M^1 - M^2 trigones are posteriorly closed by a metaloph. $AW < PW$ on M^1 but $AW > PW$ on M^2 . The hypocone is not developed, only the ridge is present on the deeply excavated hypoconal flange. The posterior margin is hardly concave. The very long mandibular incisor is bicusculate, but a minute third cuspule originates behind the second one in many specimens. In the black coloured specimens the cusps are whitely pigmented. Cingulum is not appeared on the buccal side, but on the symphysal one it is present. A_1 has only one conid but A_2 seems to be two-cusped in buccal view. Broad cingulum is present on both sides of the mandibular antemolars. In M_1 - M_2 the entoconid is placed very close to the metaconid and they are contacted together by a high entoconid crest. Cingula are not too broad, but the buccal one is somewhat more developed than the lingual one. The talonid of the third lower molar is not basined, it is reduced to one conid. The cingulum is weak on both sides.

		min.	mean	max.	spec. nr.	standard error	standard deviation
I^1	L	1.93	2.04	2.13	4	0.0550	0.0712
	H	1.18	1.25	1.28	4	0.0338	0.0409
P^4	LL	1.03	1.08	1.28	6	0.0389	0.0495
	BL	1.51	1.57	1.63	6	0.0367	0.0411
	W	1.50	1.61	1.68	6	0.0611	0.0670
M^1	LL	1.48	1.53	1.60	6	0.0367	0.0412
	BL	1.45	1.49	1.55	6	0.0233	0.0304
	AW	1.53	1.58	1.63	6	0.0322	0.0359
	PW	1.64	1.69	1.73	6	0.0217	0.0279
M^2	LL	1.33	1.37	1.43	6	0.0256	0.0325
	BL	1.35	1.41	1.48	6	0.0389	0.0446
	AW	1.60	1.67	1.73	6	0.0383	0.0435
	PW	1.50	1.55	1.65	6	0.0411	0.0506
M^3	L	0.65	0.70	0.75	4	0.0250	0.0354
	W	1.25	1.30	1.33	4	0.0300	0.0332
I_1	L	3.56	3.84	4.00	6	0.1344	0.1571
	H	0.84	0.86	0.91	6	0.0211	0.0243
M_1	L	1.48	1.58	1.65	10	0.0470	0.0531
	W	0.88	0.95	1.00	10	0.0360	0.0419
M_2	L	1.38	1.44	1.53	10	0.0480	0.0540
	W	0.80	0.88	0.98	10	0.0320	0.0445
M_3	L	1.13	1.14	1.18	9	0.0165	0.0445
	W	0.63	0.68	0.86	9	0.0165	0.0201

Table 8. Measurements of *Blarinella dubia* (BACHMAYER & WILSON, 1970) from Polgárdi 5.

Remarks. The living Asian *Blarinella quadratauda* MILNE-EDWARDS, 1872 and the fossil European *Blarinella europaea* REUMER, 1984 are also ranged in this genus. *B. dubia* is one of the typical Late Miocene and Early Pliocene (Ruscinian) Soricinae shrew of Europe, but its First Appearance Date (FAD) is problematical. KRETZOI et al. (1976) and after them RABEDER (1985) and KORDOS (1991) reported this species from the Early Vallesian localities of Rudabánya (Hungary), but ZIEGLER & MÉSZÁROS (1998) who studied an other sample from Rudabánya could not find it in the site.

Genus *Zelceina* SULIMSKI, 1962

Type species. *Neomys soriculoides* SULIMSKI, 1959.

Zelceina soriculoides (SULIMSKI, 1959)

Text-Fig. 5, Pl. 2, Fig. 8

- 1959 - *Neomys soriculoides* n. sp. - SULIMSKI, p. 149, pl. III, figs 4 a-c, figs 5 c-d (Weze 1)
 1960 - cf. *Neomys* sp. - Kowalski, p. 169 (Rebيلية Królewskie)
 1962 - *Zelceina soriculoides* (SULIMSKI, 1959) - SULIMSKI, p. 478, figs 2, 3a-c (Weze 1)
 1964 - *Neomys soriculoides* (SULIMSKI, 1959) - KOWALSKI, p. 77 (Weze 1)
 1984 - *Zelceina soriculoides* (SULIMSKI, 1959) - REUMER, p. 74, pl. 23, figs 1-7 (Csarnóta 2)
 1990 - *Zelceina soriculoides* (SULIMSKI, 1959) - RZEBIK-KOWALSKA, p. 69, fig. 9 (Weze 1, Rebيلية Królewskie)

Type material. 1 rostral part of a skull with the complete dentition, 1 left mandible, 1 right mandible, No 160, 700, 119, SULIMSKI 1959, p. 149 fig. 5 c-d, Type locality: Weze 1, Poland, Pliocene, MN 15.

Stratigraphical range. Late Miocene (Turolian, MN 13) - Pliocene (Ruscinian, MN 16), Middle Europe.

Studied material. Polgárdi 4: 3 right and 4 left mandible fragments. Figured specimen: GMH, V. 20724.

Measurements. See Tab. 9.

Description. The coronoid process of the mandible is high, its anterior margin is concave, the posterior one has an undulation in some specimens. The coronoid process is very short. The external temporal fossa, with deep upper part, reaches downwards to the level of the upper sigmoid notch. The undivided internal temporal fossa extends upwards to the middle of the coronoid process. The upper condylar facet is cylindrical, the lower one is elongated, the interarticular area is narrow. The mental foramen is placed under the re-entrant valley of M_1 , the mandibular one under the middle or the posterior part of the internal temporal fossa. The mandibular incisor is bicusplute, the apex is sharp and curved, both cusplutes are placed far anteriorly, the posterior part of the tooth is elongated. The buccal cingulum surrounds the posterior part, the

symphysial one reaches along the posterior and the inferior margins. The two-cusped A_2 has well-developed buccal and lingual cingula. The entoconid crest is moderately high in M_1 - M_2 , the cingulum is present on both sides. The talonid of the third molar is narrow, but slightly basined, with two conids.

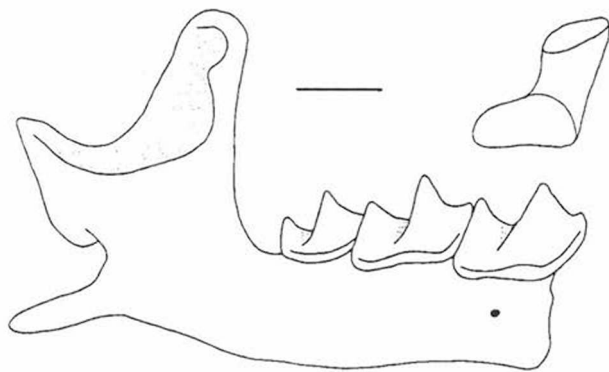


Fig. 5. *Zelceina soriculoides* (SULIMSKI, 1959). GMH V. 20724., loc. Polgárdi 4 "lower", right mandible fragment with M_1 - M_3 , lateral view and the condyle, posterior view; scale bar = 1 mm.

Remarks. RZEBIK-KOWALSKA (1990) described a smaller and more primitive *Zelceina* from the Early Ruscinian of Poland, as *Z. podlesicensis*. She suggested that this form could be an ancestor of *Z. soriculoides*. The recent researches extend the stratigraphical range of the studied species. The Polgárdi occurrence is the European FAD of the genus, thus the mentioned genealogy is unproved. One further species (*Zelceina kormosi*) is reported from Asia, which "seems more closely related to *Z. podlesicensis*" than to *Z. soriculoides* (STORCH 1995).

		min.	mean	max.	spec. nr.	standard error	standard deviation
I_1	L	2.78	2.79	2.80	2	-	-
	H	0.73	0.77	0.80	2	-	-
M_1	L	1.40	1.43	1.50	4	0.0375	0.0433
	W	0.80	0.85	0.88	4	0.0325	0.0342
M_2	L	1.23	1.28	1.33	5	0.0224	0.0319
	W	0.75	0.77	0.81	5	0.0248	0.0258
M_3	L	1.01	1.03	1.06	5	0.0192	0.0206
	W	0.58	0.61	0.63	5	0.0168	0.0185

Table 9. Measurements of *Zelceina soriculoides* (SULIMSKI, 1959) from Polgárdi 4.

Tribe Soriculini KRETZOI, 1965
Genus *Asoriculus* KRETZOI, 1959

Type species. *Asoriculus gibberodon* (PETÉNYI, 1864).

Asoriculus gibberodon (PETÉNYI, 1864)
Pl. 1, Fig. 4, Pl. 2, Fig. 9

- 1864 - *Crocidura gibberodon* PETÉNYI - PETÉNYI, pl. 1, fig. 7 (Beremend)
1934 - *Soriculus kubinyii* n. sp. - KORMOS, p. 303, fig. 36 (Villány 3)
1937 - *Soriculus kubinyii* KORM. - KORMOS, p. 1090 (Villány 3)
1956 - *Soriculus gibberodon* (PETÉNYI) (= *Soriculus kubinyii* KORMOS) - KRETZOI, pp. 61, 184 (Villány 3)
1959 - *Soriculus* (*Asoriculus* n. sg.) *gibberodon* (PETÉNYI) - KRETZOI, pp. 238, 245 (Csarnóta 2)
1962 - *Asoriculus gibberodon* (PETÉNYI) - KRETZOI, pp. 301, 342 (Csarnóta 2)
1973 a - *Episoriculus gibberodon* (PETÉNYI) - JÁNOSSY, p. 102 (Osztramos 7)
1973 b - *Episoriculus tornensis* sp. n. - JÁNOSSY, p. 50, pl. 1, figs 1, 10 (Osztramos 13)
1973 b - *Episoriculus borsodensis* sp. n. - JÁNOSSY, p. 53, pl. 1, figs 5, 9, 13 (Osztramos 1)
1974 - *Episoriculus tornensis* JÁNOSSY - JÁNOSSY, p. 18 (Osztramos 9)
1977 - *Episoriculus borsodensis* JÁNOSSY - JÁNOSSY & KORDOS, p. 41 (Osztramos 1)
1977 - *Episoriculus gibberodon* (PETÉNYI) - JÁNOSSY & KORDOS, p. 47 (Osztramos 7)
1977 - *Episoriculus tornensis* JÁNOSSY - JÁNOSSY & KORDOS, p. 51 (Osztramos 13)
1978 - *Episoriculus gibberodon* (PETÉNYI) - JÁNOSSY, p. 69 (Osztramos 7)
1979 - *Episoriculus gibberodon* (PETÉNYI) - JÁNOSSY, pp. 23, 27, 34 (Csarnóta 2, Osztramos 7, Villány 3)
1981 - *Episoriculus borsodensis* JÁNOSSY, 1973 - RZEBIK-KOWALSKA, p. 236, figs 3-4 (Podlesice)
1981 - *Episoriculus gibberodon* (PETÉNYI, 1864) - RZEBIK-KOWALSKA, p. 245, fig. 6 (Weze 1)
1984 - *Episoriculus gibberodon* (PETÉNYI, 1864) - REUMER, p. 92, pl. 27, figs 3-11, pl. 28, figs 1-12, pl. 29, figs 1-4, pl. 30, figs 1-4, pl. 31, figs 1-2 (Osztramos 1, 7, 9, 13, Csarnóta 2, Villány 3)
1994 - *Episoriculus gibberodon* (PETÉNYI, 1864) - RZEBIK-KOWALSKA, p. 81 (Podlesice, Zamkowa Dolna A, B, Zalesiaki 1 B, Weze 1, Rebielice Królewskie 1A, 2, Kielniki 3 B)
1995 - *Asoriculus gibberodon* (PETÉNYI, 1864) - DOUKAS et al., p. 58, pl. 7, figs 1-4 (Maramena)
1998 a - *Episoriculus gibberodon* (PETÉNYI, 1864) - MÉSZÁROS, p. 108, pl. 3, figs 1-11 (Tardosbánya)

Neotype. A skull with nearly complete dentition, GMH - OB. 3685., KORMOS (1934), p. 304, fig. 36. Type locality: Beremend (Hungary, Early Villányian, MN 16), neotype locality: Villány 3 (Hungary, Late Villányian, MN 17).

Stratigraphical range. Late Miocene (Turolian, MN 12) - Pliocene (Villányian, MN 17)

Studied material. Polgárdi 4: 1 fragmentary skull, 41 left and 32 right mandibles, 6 left and 5 right maxillary fragments, 1 left I¹, 1 right M¹. Figured specimens: GMH, V. 20722.

Measurements. See Tab.10.

		min.	mean	max.	spec. nr.	standard error	standard deviation
I ¹	L	-	3.88	-	1	-	-
	H	-	1.06	-	1	-	-
P ⁴	LL	0.80	0.87	0.93	7	0.0331	0.0406
	BL	1.26	1.40	1.50	7	0.0669	0.0792
	W	0.90	1.27	1.46	7	0.2114	0.2364
M ¹	LL	1.30	1.38	1.48	7	0.0359	0.0508
	BL	1.33	1.37	1.43	7	0.0265	0.0316
	AW	1.33	1.41	1.5	7	0.0465	0.0547
	PW	1.49	1.54	1.58	7	0.0371	0.0393
M ²	LL	-	1.05	-	1	-	-
	BL	-	1.15	-	1	-	-
	AW	-	1.50	-	1	-	-
	PW	-	1.34	-	1	-	-
I ₁	L	2.89	2.90	2.92	2	-	-
	H	0.80	0.80	0.81	2	-	-
M ₁	L	1.15	1.46	1.58	8	0.0978	0.1304
	W	0.76	0.83	0.90	8	0.0375	0.0474
M ₂	L	1.20	1.35	1.48	9	0.0630	0.0785
	W	0.68	0.79	0.95	9	0.0635	0.0789
M ₃	L	0.95	1.06	1.18	8	0.0643	0.0704
	W	0.53	0.61	0.70	8	0.0338	0.0020

Table 10. Measurements of *Asoriculus gibberodon* (PETÉNYI, 1864) from Polgárdi 4.

Description. The coronoid process of the mandible is high, with concave anterior margin. The interarticular area of the condyle is narrow, the upper articular facet is cylindrical, the lower one is strongly elongated in lingual direction. The mandibular foramen is situated under the posterior part of the internal temporal fossa. The mental foramen is below the protocone of the M₁ or somewhat behind it (at the re-entrant valley). The internal temporal fossa relatively to the coronoid process is small and narrow, or continues upwards as a shallow groove into the upper part of the process. The mandible is elongated, the lower margin of the horizontal ramus is concave. The upper incisor is slightly fissident. The dorsal and the posterior margins form a sharp angle. The convex posterior margin is provided with a broad cingulum. The top of the talone is sharp. The P⁴ parastyle is protruding, it is connected to the high paracone by a narrow parastylar crest. The protocone is separated from the well-developed hypocone by a valley. The hypoconal flange is bordered by a high ridge, the posterior margin is deeply notched. The M¹ protocone and the hypocone are separated by a wide valley. All the cones of the trigone are well developed, the trigone basin is very deep. The talone is short, because the posterior margin is deeply notched. AW < PW, the parastyle is shorter than the metastyle. M² is a morphologically very similar tooth to the previous one, but AW > PW and the metastyle is about same sized as the parastyle. There are two cuspules behind the sharp, up-turned apex of the lower incisor. The anterior cuspule is slightly developed, but the posterior one is high. A buccal cingulum runs along the whole basal margin of the tooth. The lower antemolars are provided with cingula on both sides. There is only one cusp in A₁, but A₂ is two-cusped. The entoconid crest is present in M₁-M₂. The lingual end of the postcristid and the

entoconid are separated by a deep valley. The cingula are present either on the buccal or the lingual sides. Weak buccal and lingual cingula are present in the third lower molar. The talonid is basined and both conids are visible on the posterior margin.

Remarks. The type material of *Crocidura gibberodon* PETÉNYI 1864 (Beremend, Hungary) has been lost. KORMOS (1934) described the same species from the Hungarian Villány 3 site as *Soriculus kubinyii*. Its type material is stored in the collections of the Geological Museum of Hungary. KRETZOI (1962) classified the species as *Asoriculus*. REPENNING (1967) ranged it in *Episoriculus* and this classification became widely accepted. JÁNOSSY (1973) described two new species, *E. tornensis* and *E. borsodensis* from Osztramos. RZEBIK-KOWALSKA (1981) thought possible that all European *Episoriculus* forms belong to *E. gibberodon*. REUMER (1984) included all Hungarian forms in *Episoriculus gibberodon*. HUTTERER (1994) excluded all fossil forms from genus *Episoriculus*, so *Asoriculus* KRETZOI, 1959 is the valid name for *gibberodon*.

Subfamily and tribe Soricidae incertae sedis
Genus *Paenelimnoecus* BAUDELLOT, 1972

Type species. *Paenelimnoecus crouzei* BAUDELLOT, 1972.

Paenelimnoecus repenningi (BACHMAYER & WILSON) 1970
Text-Fig. 6, Pl. 2, Fig. 5

- 1911 - *Sorex* sp. - KORMOS, p. 57 (Polgárdi 2)
1954 - *Soricidarum* g. et sp. indet. I. - KRETZOI, p. 49. (Csákvár)
partim 1954 - *Soricidarum* g. et sp. indet. II. - KRETZOI, p. 49. (Csákvár)
1970 - *Petenyiella ? repenningi* n. sp. - BACHMAYER & WILSON, p. 549, figs 7, 32, 32a, 33, 50, 50a (Kochfidish)
1978 - *Petenyiella ? repenningi* - BACHMAYER & WILSON, p. 139, fig. 3 (Kochfidish)
1984 - *Petenyiella repenningi* BACHMAYER & WILSON, 1970 - KRETZOI, p. 216 (Sümeg)
1996 - *Paenelimnoecus repenningi* (BACHMAYER & WILSON, 1970) - MÉSZÁROS, p. 15, pl. 4, figs 7 a-d (Sümeg, Csákvár)
1988 a - *Paenelimnoecus repenningi* (BACHMAYER & WILSON, 1970) - MÉSZÁROS, p. 109, pl. 4, figs 1-10 (Tardosbánya)

Holotype. Left lower jaw fragment with M₁-M₃, NHMV, Div. Geol. Paleont., 1970/1388. (BACHMAYER & WILSON 1970, p. 549, fig. 33.) Type locality: Kohfidisch (Austria, Late Vallesian, MN 10).

Stratigraphical range. Late Miocene (Early Vallesian, MN 9 - Late Turolian, MN 13), Europe.

Studied material. Polgárdi 4: 7 left and 15 right mandibles. Polgárdi 2: 1 right mandible fragment. Figured specimens: GMH, V. 20725.

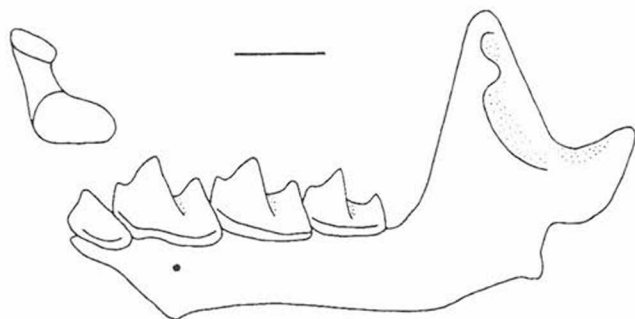


Fig. 6. *Paenelimnoecus repenningi* (BACHMAYER & WILSON, 1970). GMH V. 20725., loc. Polgárdi 4 "upper", left mandible fragment with A₂-M₃, lateral view and the condyle, posterior view; scale bar = 1 mm.

		min.	mean	max.	spec. nr.	standard error	standard deviation
I ₁	L	-	2.30	-	1	-	-
	H	-	0.56	-	1	-	-
M ₁	L	1.18	1.23	1.29	9	0.0388	0.0412
	W	0.65	0.72	0.95	9	0.0573	0.0848
M ₂	L	1.06	1.18	1.26	11	0.0367	0.0507
	W	0.56	0.69	0.95	11	0.0655	0.0954
M ₃	L	0.83	0.90	0.93	10	0.0284	0.0331
	W	0.48	0.58	0.70	10	0.0688	0.0767

Table 11. Measurements of *Paenelimnoecus repenningi* (BACHMAYER & WILSON, 1970) from Polgárdi 4.

Measurements. See Tab. 11.

Description. The coronoid process is high and narrow, its top is rounded, the anterior margin is concave. The coronoid spicule is small, the external temporal fossa usually extends downwards to the middle of the condyle. The upper facet of the condyloid process is oval, the interarticular area is short and narrow. The internal temporal fossa is triangular or subtriangular and higher than wide. Its lower margin is horizontal or ascending backwards. The mandibular foramen is placed under the middle or the posterior part of the fossa, the mental one under the re-entrant valley of M₁. There is no cingulum on the buccal side of the bicusculate mandibular incisor. In buccal view a small extra conid is visible behind the main conid of the lower anteromolars. A₁ is far smaller than A₂. Entoconid crest is not appeared in M₁-M₂. The buccal and lingual cingula are weak. The talonid of M₃ is reduced to a single cusp. Weak cingulids are present both on the buccal and lingual sides.

Remarks. The subfamilial and tribal status of *Paenelimnoecus* is problematic. REUMER (1984) arranges it in the Allosoricini, then (1992) in the Allosoricinae, and gives a new diagnosis for the re-established subfamily. STORCH (1995) sees little justification for the inclusion of *Paenelimnoecus* in Allosoricines and ranges the taxon in Soricinae and leaves the tribal allocation open.

By this time four European and one Asian species are known from the genus *Paenelimnoecus*. *P. micromorphus* occurred in the MN 3 and 4 Zones of SW-Germany. *P. crouzei* was found in SW-France (MN 6) and Turkey (MN 8). *P. repenningi* thrives out the whole Late Miocene of Middle Europe (Hungary, MN 9-13, Austria, MN 10). *P. pannonicus* (KORMOS) is recorded from the Pliocene of Hungary, Romania and Poland (MN 14-16). *P. obtusus* (Inner Mongolia, China, MN 13) represents the only extra-European record of this genus. On the basis of the morphology, the specimens under discussion are classified as *P. repenningi*.

Discussion

Biostratigraphy

KORDOS (1991 a), on the basis of the cricetid remains correlated the Polgárdi karstic cavity fills with the Late Turolian MN 13 Zone, but noted that locality 2 is somewhat younger than the entirely contemporaneous others. This view is supported by the shrews. The exclusive attendance of the subfamily Soricinae and the occurrences of the typical Late Miocene elements (*Crusafontina*, *B. dubia*, *P. repenningi*) in the faunas make us sure that the assemblages can be correlated with the Late Miocene (Vallesian and Turolian). The presence of *C. kormosi* indicates younger age than the Vallesian Sümeg locality (MN 10), and its measurements suggest that the faunas are later than Tardosbánya (MN 12) (MÉSZÁROS 1998 b). According to MÉSZÁROS (1998 a) the first appearance of *Asoriculus gibberodon* is in Tardosbánya, thus its Polgárdi appearance dates the sites after the MN 11/12 boundary. According to the results of the present studies *Zelceina* and *Kordosia* emerge in the MN 13 Zone.

Thus, the shrew occurrences correlate Polgárdi 4 with the MN 13 Zone. It is separated from the MN 12 Zone by the emergence of *Zelceina*. It is older than Polgárdi 2, where *Crusafontina* is already disappeared. The appearance of *Kordosia* in Polgárdi 2 suggests somewhat younger age than Polgárdi 4, but the great difference between the two faunas seems to be rather ecological than stratigraphical. Because the stratigraphical order of locality 2 and 5 cannot be cleared by shrews, we accept the stratigraphical classification of KORDOS (1991) that Polgárdi 2 is younger than the other sites.

Stage	MN	Locality	Soricidae species						
			1	2	3	4	5	6	7
T u r o l i a n	13	Polgárdi 2 Polgárdi 5 Polgárdi 4	■	■	■	■	■	■	■
	12			■	■	■	■	■	■
	11				■				

Fig. 7. Soricidae occurrences in the Polgárdi localities. 1 - *Blarinella dubia*, 2 - *Paenelimnoecus repenningi*, 3 - *Crusafontina kormosi*, 4 - *Amblycoptus oligodon*, 5 - *Asoriculus gibberodon*, 6 - *Zelceina soriculoides*, 7 - *Kordosia topali*

Taphonomy

The Polgárdi fossil assemblages enable detailed taphonomical researches, but that would require a special project. Herein only an overview of the modifications, apparent on the shrew bones and teeth, is presented.

The white and tawny tone of the bones could have been caused by siliceous and ferruginous mineralizing solutions. The black coloration of many remains indicates periodic soil-wash into the karstic cavity. Humine acids produced in-cave-corrosion on few mandibles. The material is excellently preserved, a great majority of the teeth are in situ. Digested enamel is recorded in few specimens, but their amount is negligible in the great number of the fossils. The relative frequency of isolated teeth is very low. Nearly all humeri in the microbone samples came from juvenile animals (M. ARMOUR-CHELU, pers. comm.)

The taphonomic features of the Polgárdi 4 and 5 assemblages suggest principally pit-fall accumulations. Most of the soricids were fallen alive into the fissures. The shrews could hardly escape from the deep pits: they die in the moment when they are ambushed, or - because of their remarkably fast metabolism - a short time after. Some in-cave bone movements before the fossilisation is marked by the breakage of the extraordinarily fragile bones (for example the aboral part of the skull).

KORMOS (1911), by the multitudinous occurrence of the micromammal bones, presumed predator birds to deposit the fossil assemblage of Polgárdi 2. The present studies did not find digestive corrosion caused by the bird's stomach on the shrew bones and teeth from the classical site. As far as we can restore it from the sketch of KORMOS (1911), the micromammals came from a perpendicular, chimney-like branch of the cave, which would have permitted pit-fall accumulation.

The way of deposition of the Polgárdi vertebrate fossils is particular not only taphonomically but also paleoecologically. The high species diversity difference between localities 4 and 5 necessitates detailed ecological analysis (see below). The pit-

fall accumulations usually give unselective samples from the ancient faunas, and it is a good chance to study the species composition.

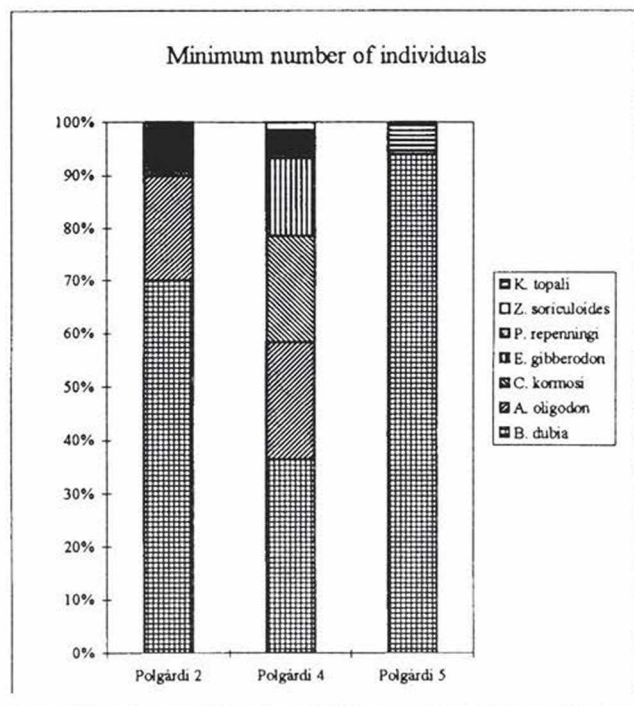


Fig. 8. Species diversity of the Polgárdi Soricidae faunas.

Palaeoecology

We apply two different methods to answer the paleoecological questions about the studied localities.

The subfamily composition of the soricid faunas gives information on the climate. The extant Crocidosoricinae and Heterosoricinae are adapted to more humid climate with balanced temperature than the recent Soricinae. The two living European subfamilies differ mainly in their preferences concerning humidity: Crocidurinae are adapted more arid conditions than Soricinae. Besides, soricines can abide colder environments and higher altitudes above sea level than crocidurines (RZEBIK-KOWALSKA, 1995).

The generic analysis of the Soricidae communities comes in useful in the determination of the biocenoses in which they lived. For the paleoecological availability of the shrew genera, if they are still living, we have to know their recent cenological preference. If the group is extinct, we need localities with known paleoecology to define its habitats.

Climate

Because of the climatic turnover, there was a great change in the Soricidae fauna of Europe during the Late Miocene (RZEBIK-KOWALSKA 1995). The somewhat colder and most arid climate caused lower diversity, then disappearance of Crocidosoricinae and Heterosoricinae shrews, with immigration of Soricinae ones. The great species number of the European soricines appears simultaneously with the coming up of the Hipparion fauna. While the larger mammals and rodents indicate mainly a steppe vegetation in the Late Miocene of the Pannonian Basin, the soricids suggest not so open environments. Their occurrences in most cases are related to somewhat more humid microclimates in mountain areas or by local water bodies.

The lack of subfamilies Heterosoricinae and Crocidosoricinae and the great diversity of the Soricinae in Polgárdi indicate herein more continental climate than in the Middle Miocene. The absence of the Crocidurinae suggest that the weather conditions were not so dry as in some periods of the Pliocene and the Pleistocene.

Habitat

On the basis of their very close relation to the extant *Anourosorex squamipes*, living in the mountain forests of SE-Asia, *Amblycoptus* and *Crusafontina* may be indices of well watered, forested environments. The very similarly evolved dentition of *A. oligodon* suggests adaptation to such malacophagous diet as the recent *Anourosorex*. *Crusafontina* is described from wooded or at least partly wooded areas. Rudabánya should have been a basin of a relatively large area with diversified vegetation, including also forests (KORDOS, 1982). STORCH (1978) mentioned Dorn-Dürkheim as a well watered, forested biotope. Although, BACHMAYER & WILSON (1970) described Kohfidisch as a largely open grassland, but with local bodies of water and restricted woodland areas.

The palaeoecology of *Kordosia*, the third recorded Anourosoricini from Polgárdi, is more problematic. While REUMER (1984) supposed this species to had been living in forested areas, by its peculiar attendance in Polgárdi 5, we should accept *Kordosia topali* as a suggestive of somewhat more open environment. Osztramos 1, from where *K. topali* was first described, was a "mixed nature with forests prevailing over the steppeic vegetation" (JÁNOSSY 1972). Its close relations to *Kordosia jessiae*, described by DOUKAS (DOUKAS et al. 1995) from the Mediterranean area, proofs that *Kordosia topali* would have preferred similar climate. However DOUKAS et al. (1995) determined Maramena, the type locality of *K. jessiae* as forested area, thus we can suppose that in its occurrence *Kordosia* insisted rather on temperature, than on vegetation. Because of its markedly southern geographical position, the Mediterranean-like warm microclimate can grow up only the south-facing, open mountain-sites in the Carpathian Basin. In this *Kordosia* can mark forests in the Mediterranean, while open fields in the northern regions. Its occurrences in the Carpathian Basin should not indicate climatic changes, but special habitat in the surroundings of the locality (see below).

Paenelimnoecus is an extinct genus, while the recent *Blarinella* lives in the mountain woods in Asia. *P. repenningi* and *B. dubia* occur in the Hipparion fauna of

the European Late Miocene, but usually in local wooded areas, mentioned also for *Crusafontina*. However we can suppose that *Blarinella* could make a living also in different habitats in the Middle Miocene, because it is present even in Polgárdi 2, a locality where any forest forms are lacking.

According to REUMER (1984) *Episoriculus* (*Asoriculus*) *gibberodon* indicates the presence of open water with a good covering of wooded vegetation.

Microclimatic events

The palaeoecology of Polgárdi raises some interesting problems. KORDOS (1991 a), on the basis of the Cricetidae fauna, correlated all the three sites with the MN 13 Zone, but noted that localities 4 and 5 are from same age, while locality 2 is somewhat younger than the previous ones. However, the shrew composition of Polgárdi 4 and 2 is particularly similar (and by the *Crusafontina*, *Paenelimnoecus*, *Amblycoptus* and *Asoriculus* occurrence, indicates wooded vegetation), while the soricid community of Polgárdi 5 is significantly different. Only *Blarinella dubia* is the common form with the others and, with the here first appeared *Kordosia topali*, the number of the species is only two. The diversity of the fauna is strongly decreased from site 4 to 5 (from six to two species).

Because of the great quantity of the bones and teeth from site 5, this phenomenon could not be explained by the accidental lost of some species under the deposition, the fossilization or the collection. The disappearance of some forest shrews could be caused by chance rather in the somewhat poorer material from site 2. The definitely different age of locality 5 from the other sites is out of the question by the stratigraphical classification of KORDOS (1991 a), based on Cricetidae, which correlated all Polgárdi localities with the Late Turolian MN 13 Zone. The taphonomical features exclude the opportunity of selective accumulation, because the little animals usually fall into the natural pits without selection and the specific composition of the fossil assemblage is the same as that of the ancient community. We cannot suppose biogeographical barrier between sites 4 and 5, because they are close together, both are parts of the same cave system. Most probably, the differences between the Polgárdi Soricidae faunas are by ecological causes. These circumstances are well-marked by the palaeoecologically very useful pit-fall samples.

The differences in the shrew species composition should not indicate macroclimatic, rather - geologically very fast - microclimatic events. These changes might be caused by the disappearance of the wooded environment (site 4) from a karst region, decreasing also the shrew diversity. Appearing of a more open nature would have resulted somewhat warmer climate, where Mediterranean faunas and floras could live, as we can see in some open karst fields in southern Hungary recently as well (for example Szársomlyó Hill, Villányi Mountains). *Blarinella*, which we have to see as a very successful "opportunistic" genus in the Late Miocene, is further present, the forest-preferring genera are disappeared, and the warm-adapted, Mediterranean *Kordosia* emerges (site 5). After a long (but geologically short) period, according to the general succession of the secondary grasslands, denser vegetation developed in the limestone hill, in which forest genera (*Paenelimnoecus* and *Amblycoptus*) could live again (site 2).

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PLATES

Plate 1

- Figs 1-3. *Blarinella dubia* (BACHMAYER & WILSON, 1970). GMH V. 20723.; loc. Polgárdi 4 "upper", 1 = left mandible fragment with the complete dentition, a = the horizontal ramus, lateral view; x 13; b = the dentition, buccal view; x 31; 2 = complete left mandible, a = medial view; x 13; b = the dentition, medial view; x 30; 3 = right maxillary fragment with P^4-M^3 , occlusal view; x 16.
- Fig. 4. *Asoriculus gibberodon* (PETÉNYI, 1864). GMH V. 20722., loc. Polgárdi 4 "upper", complete left mandible, lateral view; x 20.
- Fig. 5. *Paenelimnoecus repenningi* (BACHMAYER & WILSON, 1970). GMH V. 20725., loc. Polgárdi 4 "upper", left ascending ramus of the mandible, medial view; x 22.

Plate 2

- Figs 1-3. *Kordosia topali* (JÁNOSSY 1972). GMH V. 20721., loc. Polgárdi 5, 1 = left horizontal ramus of the mandible with A_1-M_2 , lateral view; x 14; 2 = right M^1 , occlusal view; x 26; 3 = left I_1 , buccal view, x 13.
- Figs 4-7. *Amblycoptus oligodon* KORMOS 1926. GMH V. 20720., loc. Polgárdi 4 "upper", 4 = left mandible fragment with A_1-M_1 , lateral view; x 19; 5 = right I^1 , buccal view; x 22; 6 = right I_1 , buccal view, x 15; 7 = right A^1 , occlusal view; x 32.
- Fig. 8. *Zelceina soriculoides* (SULIMSKI, 1959). GMH V. 20724.; loc. Polgárdi 4 "lower", left ascending ramus of the mandible, medial view; x 20.
- Fig. 9. *Asoriculus gibberodon* (PETÉNYI, 1864). GMH V. 20722., loc. Polgárdi 4 "upper", right mandible fragment with M_2 , medial view; x 30.
- Fig. 10. *Crusafontina kormosi* (BACHMAYER & WILSON, 1970). GMH V. 20718., loc. Polgárdi 4 "lower", right upper incisor, buccal view; x 23.
- Figs 11-12. *Blarinella dubia* (BACHMAYER & WILSON, 1970). GMH V. 20723.; loc. Polgárdi 4 "upper", 11 = left upper incisor, buccal view; x 34; 12 = right M_3 , occlusal view; x 70.

Plate 1

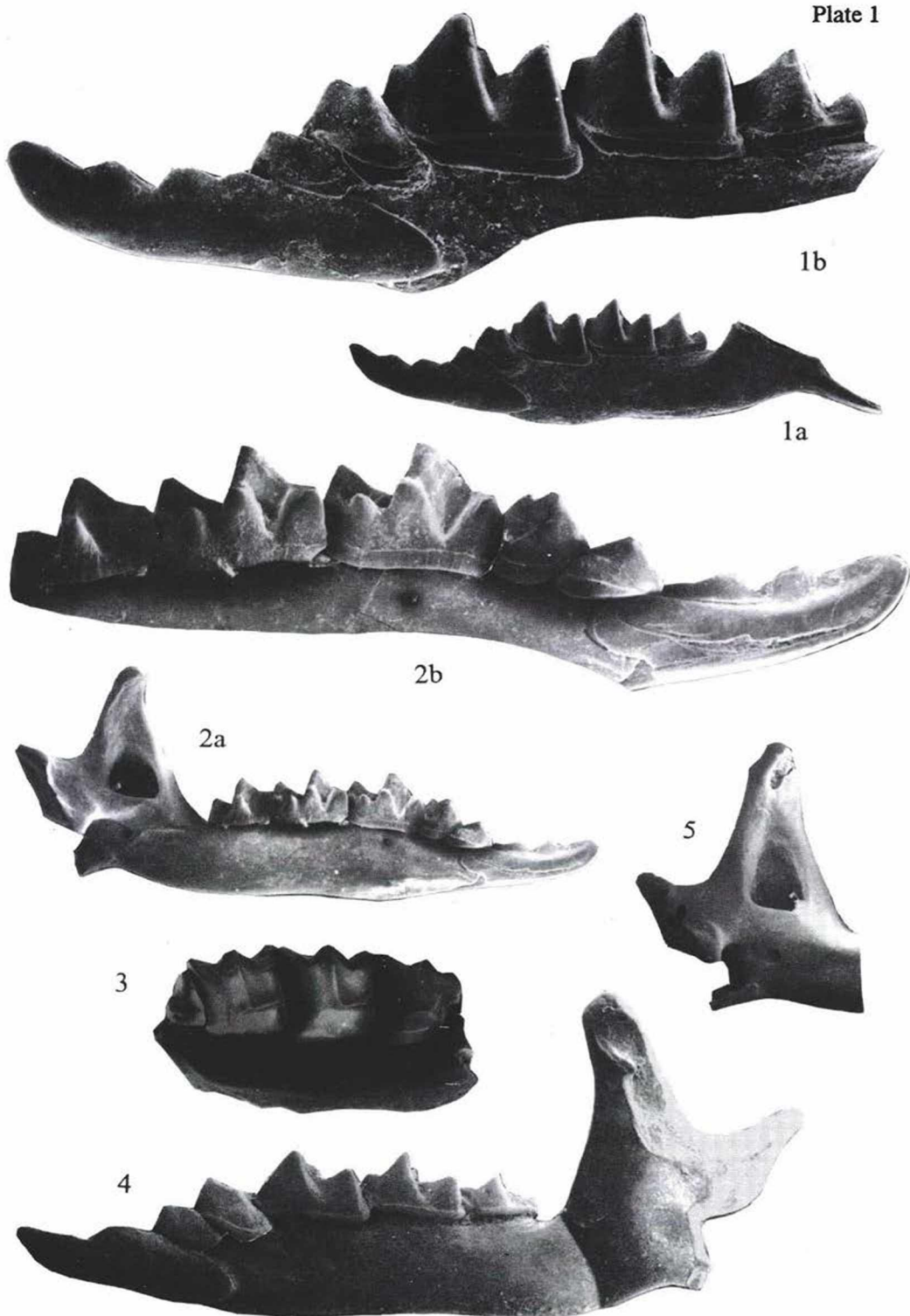


Plate 2

